# THE RELATIONSHIP BETWEEN BROOD SIZE AND AGE OF EFFECTIVE HOMEOTHERMY IN NESTLING HOUSE WRENS

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Altricial birds when hatched are not able to maintain a constant body temperature, and the ability to thermoregulate develops gradually during the first weeks of life (Dawson and Evans 1957). Many authors have investigated this developmental pattern of thermoregulation by studying the abilities of individual nestlings outside the nest. The age at which a single nestling can thermoregulate at ambient temperatures below normal body temperature could be termed the age of "physiological" endothermy, and has been determined for at least 22 species (Dunn 1975).

In nature, the pattern of thermoregulatory development might be quite different than that studied in the past in laboratories, because nest and siblings would provide insulation for the individual nestling. There is some evidence that this is true (Mertens 1969, Yarbrough 1970, M. J. Hamas pers. comm.), although no systematic study has been made to date. If insulation of nest and sibling is substantial, the age at which wild birds can thermoregulate would be advanced over the age of physiological endothermy. A lowered age of "effective" endothermy could be important to adult birds in allowing them to stop continuous brooding sooner than if the nest provided no insulation.

The following data for the House Wren (*Troglodytes aedon*) were taken to test the idea of a difference in ages of physiological and effective endothermy and to see if such a difference varied with brood size. Previous work on this species (Kendeigh and Baldwin 1928, Kendeigh 1939) provide extensive data on physiological development with which to compare my work done under natural conditions.

## MATERIALS AND METHODS

The study was carried out in June and early July 1974, near London Grove, Chester Co., Pennsylvania. Nest boxes with internal dimensions of 15 × 15 × 30 cm were placed in old fields. Wrens half filled boxes with sticks, and made a small nest cup in one corner of the box, about 5–6 cm wide and equally deep. The cup was usually lined, often with feathers and occasionally with bits of plastic bag or snake skin.

I followed growth in 8 broods. Nestlings were weighed to the nearest 0.1 g with a spring balance, and measurements to the nearest mm were made on the 7th primary (both sheath and distance from skin to tip of erupted feather) and 2 or 3 feathers each on the flank and back.

Temperature studies took place only on cool mornings (between 14 and 23°C), to avoid using boxes heated by solar radiation. Box interiors were usually only 1–2°C above ambient temperatures ($T_a$). A given nest was not investigated more than once a day.

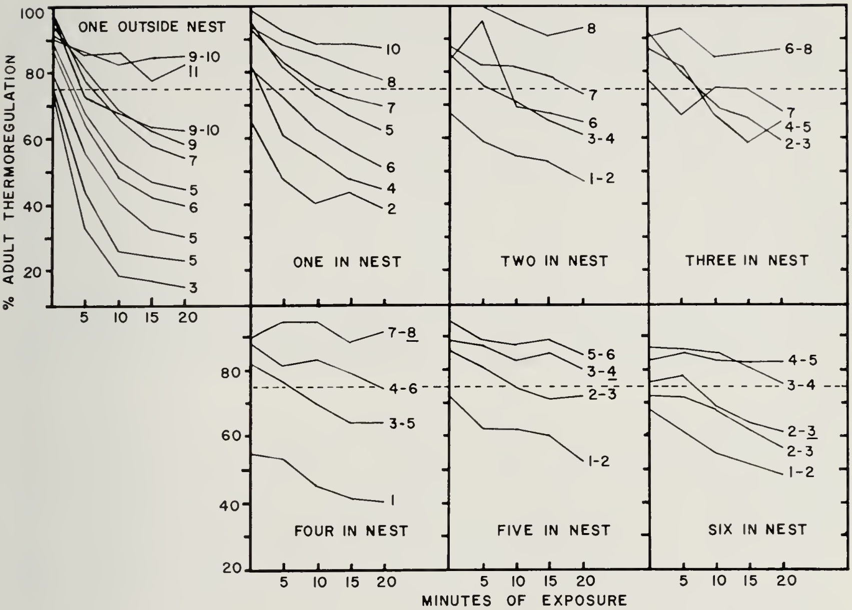

FIG. 1. Body temperature of nestlings after 5, 10, 15, and 20 min without brooding, expressed as percent of adult thermoregulation (see text). Each line represents one series of measurements on one brood. The age of nestlings involved is given at the end of each cooling curve, with the predominant age underlined where appropriate. The dotted line indicates the level of effective endothermy, defined as 75% of adult thermoregulatory abilities.

On my arrival at the nest, 3 Yellow Springs Instrument Co. telethermometer probes were immediately set up to simultaneously measure $T_a$, temperature in the nest box (at the surface of the sticks but away from the nest cup), and degrees body temperature of the nestlings ($T_b$). Readings were taken at 5 min intervals for 20 min. In most cases, initial $T_b$'s were higher than $T_b$'s after 20 min, indicating that an adult had been brooding prior to my arrival at the nest. In at least some cases, I must have arrived towards the end of the adult's inattentive period; thus, many of the periods of exposure to ambient conditions must have been longer than the 20 min of temperature readings.

Body temperature was measured by removing the nestling from the box and inserting the probe down its gullet. Although it would have been preferable to leave the nestling with inserted probe in the box throughout the measurement period, this proved impossible with the equipment at hand. Cooling through removal from the nest box was minimized, however, as I opened the box only to remove and replace the nestling, $T_b$ measurement took less than a min, and a different nestling was used each 5 min when possible.

The easiest way to present the data would be to plot cooling rate against time. However, $T_a$ differed from day to day, making thermoregulatory performances of nestlings on warm days appear to be better than they would be on cool days. Thermoregulatory

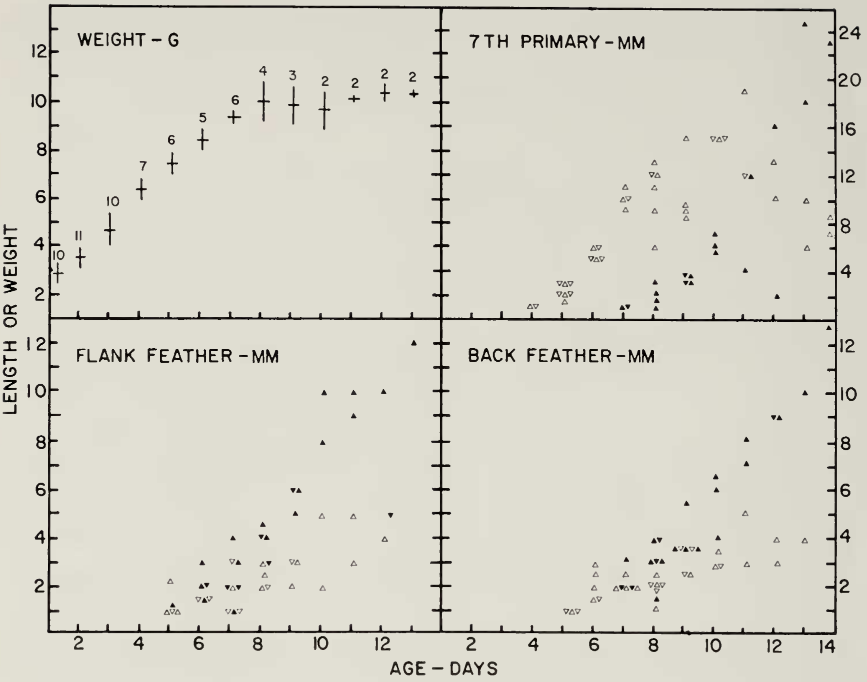

FIG. 2. Weight and feather development of House Wren nestlings. Weight data include mean (horizontal line), S.D. (vertical line), and sample size for each age. Feather lengths are shown for all individuals measured. The solid symbols show the amount of feather out of the sheath, while open symbols represent sheath length.

performance of the young was therefore standardized by expressing the difference in degrees between $T_a$ and $T_b$ as a percentage of the degrees between $T_a$ and normal adult $T_b$ (40.4°C, Baldwin and Kendeigh 1932). For example, if $T_a$ was 20.4°, and nestling $T_b$ was 30.4°, the nestling was thermoregulating 50% as well as an adult. Age of effective thermoregulation was arbitrarily defined as the age at which nestlings thermoregulated 75% as well as adults, after at least 20 min of exposure to $T_a$'s below 23°C.

## RESULTS

Figure 1 shows the results of nestling $T_b$ measurements for different ages and brood sizes. Individual nestlings outside the nest cooled rapidly for 10 min, then more slowly, with physiological endothermy occurring at about 9–10 days. These data agree well with those of Kendeigh and Baldwin (1928), giving the age of physiological endothermy as 9 days. Also in agreement with Baldwin and Kendeigh was the noticeable rise in initial $T_b$ (of young which presumably had been recently brooded) as the nestlings grew older.

TABLE 1

AGE AND WEIGHT OF HOUSE WREN NESTLINGS FROM BROODS OF DIFFERENT SIZES AT AGE OF EFFECTIVE ENDOTHERMY[a]

| | out of nest | inside nest and nest box | | | | | |
|---|---|---|---|---|---|---|---|
| Brood size | 1 | 1 | 2 | 3 | 4 | 5 | 6 |
| Age-days | 9–10[b] | 7.5 | 7.5 | 7.5 | 5–6 | 3–4 | 3–4 |
| Ave. weight (g)/nestling[c] | 9.9 | 9.5 | 7.8–8.0 | 7.3–7.7 | 6.3 | 3.3–4.0 | 3.3–4.1 |

[a] See methods for definition.

[b] Age of these nestlings was not known any closer. In all other cases, a range indicates that no additional measurements were taken to pinpoint the exact age of effective endothermy.

[c] Weights taken from actual broods whose $T_b$'s were measured, instead of from Fig. 2.

When a single nestling was left in the nest box, it was able to thermoregulate at 8 days, indicating a one day difference between ages of physiological and effective endothermy due to insulation of the nest and nest box. Although the 8- and 9-day-old young had both reached asymptotic weight, 8-day-old young had less complete feather development (Fig. 2).

When 2 or 3 nestlings were in a nest, the age of effective endothermy did not decline further (Fig. 1). Younger birds cooled more slowly in the larger brood sizes, however, and average weight per nestling was lower (Table 1). This suggests that insulation does increase with brood size, although too little to have an effect on age of effective endothermy.

Broods of 4 can effectively thermoregulate at about 5 days, when pin feathers are just beginning to appear and body weight is about ⅔ of asymptotic weight (Fig. 2). Broods of 5 and 6 thermoregulate at about 3–4 days, before feathers have even begun to appear and when body weight is only about a third of that at age of physiological endothermy.

That the age of effective endothermy does not drop progressively with the addition of each nestling may depend on the fact that nestlings in broods of 4 or more tend to lie heaped up in the nest cup in at least 2 layers, while 3 or fewer have room to lie next to each other. Surface exposure per nestling is thus much reduced in the larger broods.

## DISCUSSION

Although both parents of House Wrens feed the nestlings, only the female broods. In the first 2 days after hatching, this takes about 50% of her time during daylight hours (Kendeigh 1952), and some brooding may occur as late as 10 days after hatching. Assuming that females stop brooding once their young can effectively thermoregulate, then the mother of a brood of 6 could spend about half the number of days on the nest as a mother of 3.

This would clearly be of an advantage in freeing her to do more foraging for her larger brood. In addition, each nestling would spend less energy on keeping warm, and would require less food (Mertens 1969), lending support to Royama's (1969) ideas on the advantages of larger clutches in cold climates.

The relationship between insulation, number of young, and timing of the end of brooding is not simple. As mentioned, 2 layers of nestlings thermoregulate sooner than one layer, so the thermoregulatory advantages of adding one nestling to the brood are not the same for all brood sizes. Also, my work was done at ambient temperatures below 23°C, and nestlings were likely faced with overheating on occasion. Measurements made under these conditions might show thermal advantages for smaller broods.

Other species of birds have nests with different insulative properties and location, and have nestlings with different patterns of feather and behavioral development. There are probably numerous patterns of thermoregulatory development in the wild, adapted to different ecological conditions in each case. The subject would be well worth pursuing.

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## LITERATURE CITED

Baldwin, S. P. and S. C. Kendeigh. 1932. Physiology of the temperature of birds. Sci. Publ. Cleveland Mus. Nat. Hist. 3:1–196.

Dawson, W. R. and F. C. Evans. 1957. Relation of growth and development to temperature regulation in nestling Field and Chipping sparrows. Physiol. Zool. 30:315–327.

Dunn, E. H. 1975. The timing of endothermy in the development of altricial birds. Condor 77:288–293.

Kendeigh, S. C. 1939. The relation of metabolism to the development of temperature regulation in birds. J. Exp. Zool. 82:419–438.

———. 1952. Parental care and its evolution in birds. Ill. Biol. Monogr. 22(1–3). Univ. Ill. Press, Urbana.

——— and S. P. Baldwin. 1928. Development of temperature control in nestling House Wrens. Am. Nat. 62:249–278.

Mertens, J. A. L. 1969. The influence of brood size on the energy metabolism and water loss of nestling Great Tits, *Parus major major*. Ibis 111:11–16.

Royama, T. 1969. A model for the global variation of clutch size in birds. Oikos 20: 562–567.

Yarbrough, C. G. 1970. The development of endothermy in nestling Gray-crowned Rosy Finches (*Leucosticte tephrocotis griseonucha*). Comp. Biochem. Physiol. 34: 917–925.

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